

MOOJENICHTHYS MIRANDA-RIBEIRO
(PISCES: OSTARIOPHYSI: CHARACIDAE),
A PHYLOGENETIC REAPPRAISAL AND
REDESCRIPTION

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Abstract. — The Neotropical characiform characid genus *Moojenichthys* Miranda-Ribeiro is hypothesized to form a monophyletic lineage with *Triporthesus* Cope on the basis of shared derived features of the pectoral girdle and perhaps of the first infraorbital. Autapomorphies for *Moojenichthys* are discussed. *Moojenichthys myersi* Miranda-Ribeiro, the only member of the genus, is redescribed. This species is apparently endemic to the Rio do Braço system of the state of Bahia, Brazil.

Resumo. — Uma hipótese de relações filogenéticas reunindo em um só grupo monofilético os gêneros neotropicais *Moojenichthys* e *Triporthesus*, ambos pertencentes à família Characidae e à ordem Characiformes, é formulada com base na posse em comum de caracteres derivados na cintura escapular e, possivelmente, primeiro infra-orbital. *Moojenichthys myersi* Miranda-Ribeiro, o único membro do gênero, é redescrito. Esta espécie é, aparentemente, endêmica da bacia do Rio do Braço, no estado da Bahia, Brasil, e consiste na única ocorrência de um representante da linhagem evolutiva *Triporthesus-Moojenichthys* nos rios costeiros do leste do Brasil, excluindo o rio São Francisco.

Miranda-Ribeiro (1956:546) proposed the characid genus *Moojenichthys* for a single species, *M. myersi*, first described in that publication on the basis of two specimens collected in the Rio do Braço, near Ilhéus in the state of Bahia of eastern Brazil. *Moojenichthys myersi* has a number of external anatomical features unusual within the Characiformes. Perhaps the most striking of these are its elongate, laterally flattened body, and the pronounced, laterally compressed mid-ventral keel. Although the thoracic keel is not obvious in specimens of *Moojenichthys* under 15 mm SL, mid- to large-sized individuals of the genus have a distinct mid-ventral ridge extending from the isthmus posteriorly to the origin of the pelvic fin.

In his original description of *Moojenichthys* Miranda-Ribeiro stated that the genus

was “related” to *Triporthesus* Cope (1872) and *Clupeacharax* Pearson (1924) both of which also have elongate, laterally compressed bodies characterized by varyingly developed mid-ventral keels. Miranda-Ribeiro did not explicitly state which characters lead him to propose that these species are “related,” presumably closely. It seems reasonable, nonetheless, to assume that the overall similarities in body shapes, particularly the presence of mid-ventral keels, contributed significantly to this hypothesis.

Despite the distinctive external morphology of *Moojenichthys myersi*, subsequent references to the genus and species are extremely limited. Géry (1972:55), in his key to New World characiforms, commented that *Triporthesus* and *Moojenichthys* are probably derived from *Brycon* Müller and Troschel, and on the next page pro-

posed that *Clupeacharax* is close to *Triporthus* (1972:56). More recently, Géry (1977: 346) again emphasized the similarities between *Moojenichthys* and *Triporthus*, noting, however, that the reported dentition of *M. myersi* is more reminiscent of the subfamily "Tetragonopterinae" of the family Characidae. In that publication Géry did not comment on Miranda-Ribeiro's proposal of a possible relationship between *Moojenichthys* and *Clupeacharax*, but rather segregates *Clupeacharax* in the monotypic subfamily Clupeacharacinae. Castro (1981:138), in turn, cited some external similarities between *Clupeacharax* and *Engraulisoma* Castro.

Other than for the original description by Miranda-Ribeiro (1956) and Géry's brief comments (1972, 1977), we know of no published citations of *Moojenichthys*. Similarly, the primary ichthyological literature apparently does not include records of the subsequent capture of the species. This is not surprising given that *M. myersi* is apparently endemic to the Rio do Braço system, a poorly sampled river basin that drains into the Atlantic Ocean slightly north of the city of Ilhéus in the state of Bahia, Brazil.

Recent collecting efforts in the coastal rivers of Bahia associated with our revisionary studies of the characiform families Curimatidae and Prochilodontidae, have resulted in the capture of a large series of *Moojenichthys myersi* with a much greater range of standard lengths than available to Miranda-Ribeiro. This additional material allows us to provide a detailed redescription of the genus and species. Those specimens also permit anatomical studies to evaluate previous suggestions about the relationships of *Moojenichthys*.

Methods.—All measurements are given as proportions of standard length (SL) except for subunits of the head which are presented as proportions of head length (HL). Lateral-line scale counts include all pored scales along that series, including the scales posterior of the hypural joint. Vertebral

counts were taken from radiographs, and specimens cleared and counterstained for bone and cartilage. The vertebral count includes the four vertebrae incorporated in the Weberian apparatus, and considers the fused $PU_1 + U_1$ as a single element. In counts of median and pelvic fins, lower-case Roman numerals indicate unbranched rays, and Arabic numerals indicate branched rays. The range for each meristic value of all measured specimens is presented first, with the value for the holotype indicated in square brackets. Measurements were made following the methods outlined in Fink & Weitzman (1974:1–2).

The following institutional abbreviations are used: ANSP—Academy of Natural Sciences of Philadelphia; MNRJ—Museu Nacional, Rio de Janeiro; MZUSP—Museu de Zoologia, Universidad de São Paulo; USNM—National Museum of Natural History, Smithsonian Institution, Washington, D.C.; and FFCLRP-USP—Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo.

Phylogenetic Analysis

As noted in the introductory comments, Miranda-Ribeiro (1956:546) considered *Moojenichthys*, *Triporthus*, and *Clupeacharax* to be related, albeit without specifically stating the basis for his opinion. A number of questions exist about the phylogenetic associations of these taxa, and at least in the case of *Triporthus* the species-level classification of the genus remains unsettled.

Moojenichthys myersi has been collected only in the Rio do Braço system of eastern Brazil. *Clupeacharax* includes a single species, *C. anchoveoides*, a poorly known fish reported from scattered sites ranging from Argentina (Miquelarena & Casciotta 1982:333), through Bolivia (Pearson 1924: 47) and Peru (Ortega & Vari 1986:8), to Ecuador (Stewart et al. 1987:26). *Triporthus*, a much more speciose genus well rep-

resented in museum collections, is found on both sides of the Andean Cordilleras across much of lowland South America. Miranda-Ribeiro (1941), who applied *Chalcinus* Cuvier & Valenciennes (1849) to the members of *Triporthesus*, recognized eleven species including *Chalcinus culter* Cope which Fowler (1907) segregated in the genus *Coscinoxyron*. Myers (1940:170) pointed out that *Chalcinus* was already occupied in the Hymenoptera, and that *Triporthesus* was the next available name for the members of the genus. Schultz (1944:273) and Weitzman (1960:239) agreed that Miranda-Ribeiro's revisionary effort was unsatisfactory, a view that we share. Géry (1977:343, 654) in his key to the members of *Triporthesus*, recognized only nine of the nominal species as valid, and tentatively retained *culter* in *Triporthesus*. This uncertainty concerning the recognizable species of *Triporthesus* complicates a determination of whether the genus is monophyletic. Those questions are beyond the scope of this study. We will, rather, attempt to determine the phyletic relationships of *Moojenichthys*, and critically evaluate suggestions that the genus is related to *Triporthesus* and *Clupeacharax*.

Mid-ventral keel.—One of the most obvious features of *Moojenichthys* is the distinct mid-ventral keel that extends posteriorly from the isthmus to between the origins of the pelvic fins. Whereas the posterior portion of this keel is formed by fleshy tissue, the anterior portion is underlain by asymmetrically expanded coracoid bones. The somewhat irregular anterior margins of the coracoids are relatively short where they meet the anteroventral margins of the cleithra (Fig. 1B). The dorsal margin of the coracoids in *Moojenichthys* gradually rises posteriorly to the region where it articulates with the scapula and mesocoracoid. As a consequence, the overall proportions of the plate-like ventral portion of the coracoid are distinctly asymmetrical in lateral view, with the posterior margin of the coracoid notably deeper than the anterior border of the bone.

Such asymmetrically expanded coracoids are relatively unusual within characiforms. A horizontally rectangular, moderately-sized coracoid with an overall horizontally rectangular form is found in the vast majority of characiforms of all families (e.g., Characidae (*Brycon*, Fig. 1A); Prochilodontidae, see Roberts 1973:fig. 24; Hemiodontidae, see Roberts 1974:figs. 16, 53; Lebiasinidae, see Weitzman 1964:fig 10; Parodontidae, see Roberts 1974:fig. 76; and Erythrinidae, see Starks 1930:fig. 8). Indeed, only the characiform families Characidae and Gasteropelecidae include taxa in which the coracoids are dramatically expanded to form distinct thoracic keels. Within the Characidae enlarged coracoids are absent among Old World members of the family, and the vast majority of Neotropical characids similarly lack significant expansions of these bones (e.g., *Acestrorhynchus*, see Roberts 1969:fig. 52; and *Brycon* (Fig. 1A), see also Weitzman 1962:figs. 18, 19). As noted in the introductory section, the species of *Triporthesus* are also characterized by a distinct thoracic keel. The coracoids in *Triporthesus* are similar to those of *Moojenichthys* in being asymmetrically and vertically expanded in lateral view. In *Triporthesus*, however, the dorsal margin of the plate-like ventral portion of the ossification is more steeply angled, and the posterior margin of the bone much more extensive vertically than that in *Moojenichthys* (Fig. 1C). This gives the profile of the bone a near equilateral triangular appearance. Given that most characids and non-characid characiforms lack enlarged coracoids, the common occurrence of expanded coracoids found in *Moojenichthys* and *Triporthesus* is reasonably hypothesized as a derived character which, in turn, would be congruent with the hypothesis that the two genera are sister taxa.

Expanded coracoids associated with a thoracic keel are, however, not unique to *Moojenichthys* and *Triporthesus* among characiforms. As noted in the introductory discussion, an enlargement of that element

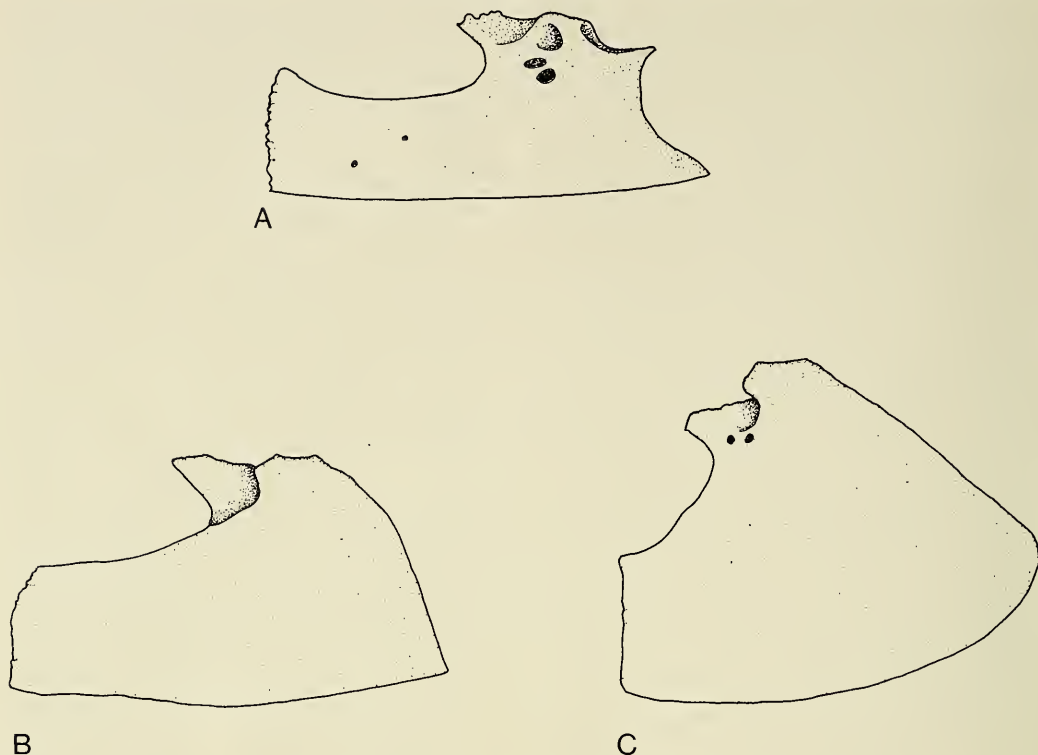


Fig. 1. Coracoids of A) *Brycon falcatus*, USNM 226161, 75.1 mm SL; B) *Moojenichthys myersi*, USNM 304497, 84.8 mm SL; and C) *Triportheus angulatus*, USNM 270343, 76.6 mm SL; right side, medial view, anterior to left.

also occurs in *Clupeacharax* and may have lead Miranda-Ribeiro to suggest that the genus was related to *Moojenichthys*. Starks (1930:22–23, fig. 9) described and figured the expanded coracoid of *Rhaphiodon* Agassiz, a genus of large predatory Neotropical characiforms. Weitzman (1960:239) noted that a keeled thorax and expanded coracoids, although unusual among characiforms (his “characids”), also occur in *Piabucus* Oken, *Pseudocorynopoma* Perugia, *Rhaphiodon*, and the genera *Carnegiella* Eigenmann, *Gasteropelecus* Pallas, and *Thoracocharax* Fowler, the last three of which together constitute the Gasteropelecidae (sensu Greenwood et al. 1966:395). Expanded coracoids also are found in *Cynodon* Spix, *Hydrolycus* Müller and Troschel and *Gnathocharax* Fowler. All of the above cited taxa appear to be surface feeders which,

with the exception of the Gasteropelecidae, also have moderately to distinctly elongate bodies.

The occurrence of expanded coracoids in a number of characid taxa other than *Moojenichthys* and *Triportheus* brings, into question the appropriateness of using that feature to propose a close relationship for those genera. Weitzman suggested (1954: 230–231) that the specialized expansions of the coracoids probably arose several times within the Characiformes. The present poor understanding of phylogenetic relationships within the Characiformes in general, and the Characidae in particular, restricts the degree to which we are able to critically evaluate that suggestion in all instances. Nonetheless, subsequent research by various researchers has yielded data that support Weitzman’s suggestion, and which in-

dicates that the occurrence of expanded coracoids in characids other than *Moojenichthys* and *Triporthus* is homoplastic relative to that feature in those genera.

Vari (1977:4–6) discussed a series of distinctive derived features of the posterior chamber of the gas-bladder and of the anterior proximal pterygiophores of the anal fin that unite *Piabucus* with *Iguanodectes* Cuvier. In *Iguanodectes* the pre-pelvic region is transversely rounded. *Pseudocorynopoma* is a member of the subfamily Glandulo-caudinae, a taxon which Weitzman et al. (1985:112–113) noted may not represent a monophyletic assemblage. Nonetheless those authors tentatively suggested that *Pseudocorynopoma* may be part of a monophyletic subset of genera within the Glandulo-caudinae. Other species in the subfamily lack keeled thoracic regions. Howes (1976) united *Rhaphiodon*, *Cynodon*, and *Hydrolycus* as a tribe, the Cynodontini, and hypothesized on the basis of a variety of characters that the lineage consisting of these three genera was most closely related to various genera of the characid tribe Characini. The Characini, in turn, consists of species in which the coracoids are not dramatically enlarged.

Thus the available evidence indicates that the characid taxa with keeled thoracic regions cited in the previous paragraph are each in turn most closely related to species or species groups without that derived modification. The species with expanded coracoids cited in the immediately preceding section also lack the derived features of the infraorbital series and lateral ethmoid common to *Moojenichthys* and *Triporthus* (see discussions in following sections). Consequently it is most parsimonious to assume that the pre-pelvic keels of *Piabucus*, *Pseudocorynopoma*, *Rhaphiodon*, *Cynodon*, and *Hydrolycus* are homoplastic relative to the expanded coracoids in *Moojenichthys* and *Triporthus*.

Information concerning the phylogenetic relationships of the Gasteropelecidae, *Clu-*

peacharax, and *Gnathocharax* is somewhat more equivocal. The three genera of the Gasteropelecidae constitute a highly derived lineage presumably derived from some component of what is now recognized as the Characidae (Weitzman 1954:243). Although the closest relatives of the Gasteropelecidae remain to be elucidated, we agree with Weitzman (1954) that the overall characters of gasteropelecids differ dramatically from those of *Triporthus* and that gasteropelecids are apparently evolved from a different subunit within the Characiformes. Although a resolution of the phylogenetic associations of gasteropelecids would require an analysis that extends far beyond the scope of this paper, one feature of the Gasteropelecidae is noteworthy relative to this question. Weitzman & Fink (1983:391) noted that the supraorbital bone is absent in all the “tetragonopterine” characids they examined. The supraorbital is widely distributed among characiforms, and also among the members of the Characidae both in the New World and Africa. The absence of that ossification is thus hypothesized to be a derived condition within the Characidae. The supraorbital is absent in the Gasteropelecidae (see Weitzman 1954:7), and the common absence of the supraorbital in “tetragonopterines” and gasteropelecids may be a derived feature indicative of common ancestry of those taxa. Both *Triporthus* and *Moojenichthys*, in contrast, retain a supraorbital.

The relationships of *Gnathocharax*, a monotypic genus of the Amazon basin with an expanded coracoid, are still unresolved. *Gnathocharax* lacks the distinct anterior process of the lateral ethmoid common to *Moojenichthys*, *Triporthus*, *Brycon*, and various other characids (see discussion under “Autapomorphies of *Moojenichthys*”). *Gnathocharax* also does not have the distinctive modification of the first infraorbital found in *Moojenichthys*, *Triporthus*, and at least some species of *Brycon*. Finally, *Gnathocharax* lacks a supraorbital and is

characterized by conical dentition typical of the characid tribe Characini and groups probably aligned with that tribe (see also discussions concerning the monophyly of the Characini by Menezes (in Sazima 1983), Vari (1986), and Weitzman & Vari (1987)). The cumulative data is congruent with the hypothesis that the coracoid expansion in *Gnathocharax* is homoplastic relative to that in *Moojenichthys* and *Triportheus*.

The phylogenetic relationships of *Clupeacharax*, the last characid genus in our list of genera with expanded coracoids are uncertain. Castro (1981:138) noted a series of similarities between *Clupeacharax* and *Engraulisoma* which has non-expanded coracoids. Ongoing studies by one of us (RMCC) are aimed at analyzing the significance of these similarities between *Clupeacharax* and *Engraulisoma*. In the interim nonetheless, several features of *Clupeacharax* bring into question the hypothesis of a close relationship between that genus and *Moojenichthys* as first proposed by Miranda-Ribeiro (1956). *Clupeacharax* lacks the derived form of the first infraorbital common to *Moojenichthys*, *Triportheus* and some species of *Brycon* (see discussion under "Infraorbitals"). Furthermore, *Clupeacharax* lacks the anterior process of the lateral ethmoid common to *Triportheus*, *Moojenichthys*, *Brycon*, and various other characids (see discussion under "Autapomorphies of *Moojenichthys*"). Thus even in the absence of a detailed analysis of the relationships of *Clupeacharax* it is more parsimonious to hypothesize that the enlargement of the coracoids in that genus are homoplastic with respect to those in *Moojenichthys* and *Triportheus*.

In summary, the presence of expanded coracoids in gasteropelecids and various characids besides *Moojenichthys* and *Triportheus*, thus appears to have arisen independently of that feature in those genera. The possession of asymmetrically vertically enlarged coracoids is consequently pro-

posed as a synapomorphy for *Moojenichthys* and *Triportheus*.

In our introductory discussion we note that Géry (1977:346) commented that the dentition of *Moojenichthys* is "approaching [that of] the Tetragonopterinae." The presence of a supraorbital in *Moojenichthys myersi* argues, however, against a close phylogenetic alignment of *Moojenichthys* with tetragonopterines in which that ossification is apparently absent (Weitzman & Fink 1983:391).

Infraorbitals.—A second possible synapomorphy for *Triportheus* and *Moojenichthys* is found in the infraorbital series. *Moojenichthys* and *Triportheus* have the series of ossifications surrounding the orbit typical for characiforms, six infraorbitals, a supraorbital, and an antorbital. The most notable feature in these series of ossifications in *Moojenichthys* and *Triportheus* involves the form of the first infraorbital and its association with the second infraorbital. The posteroventral portion of the first infraorbital in both *Moojenichthys* and *Triportheus* extends distinctly ventral of the anteroventral portion of the second infraorbital thereby significantly reducing the degree to which the latter element enters into the outer margin of the infraorbital series (Fig. 2). This association of the two anteriormost infraorbital elements differs from the morphology of these bones in *Clupeacharax*, *Rhaphiodon*, *Piabucus*, *Pseudocorynopoma*, *Carnegiella*, *Gasteropelecus*, *Thoracocharax*, *Cynodon*, *Hydrolycus*, *Gnathocharax*, the other characid genera known to have expanded coracoids. In those other taxa the first and second infraorbitals meet along a straight anteroventrally to posteroventrally aligned juncture without any invasion by the first infraorbital of the area primitively occupied by the anteroventral portion of the second infraorbital.

Although the derived form of the first and second infraorbitals in *Moojenichthys* and *Triportheus* serves to distinguish those taxa

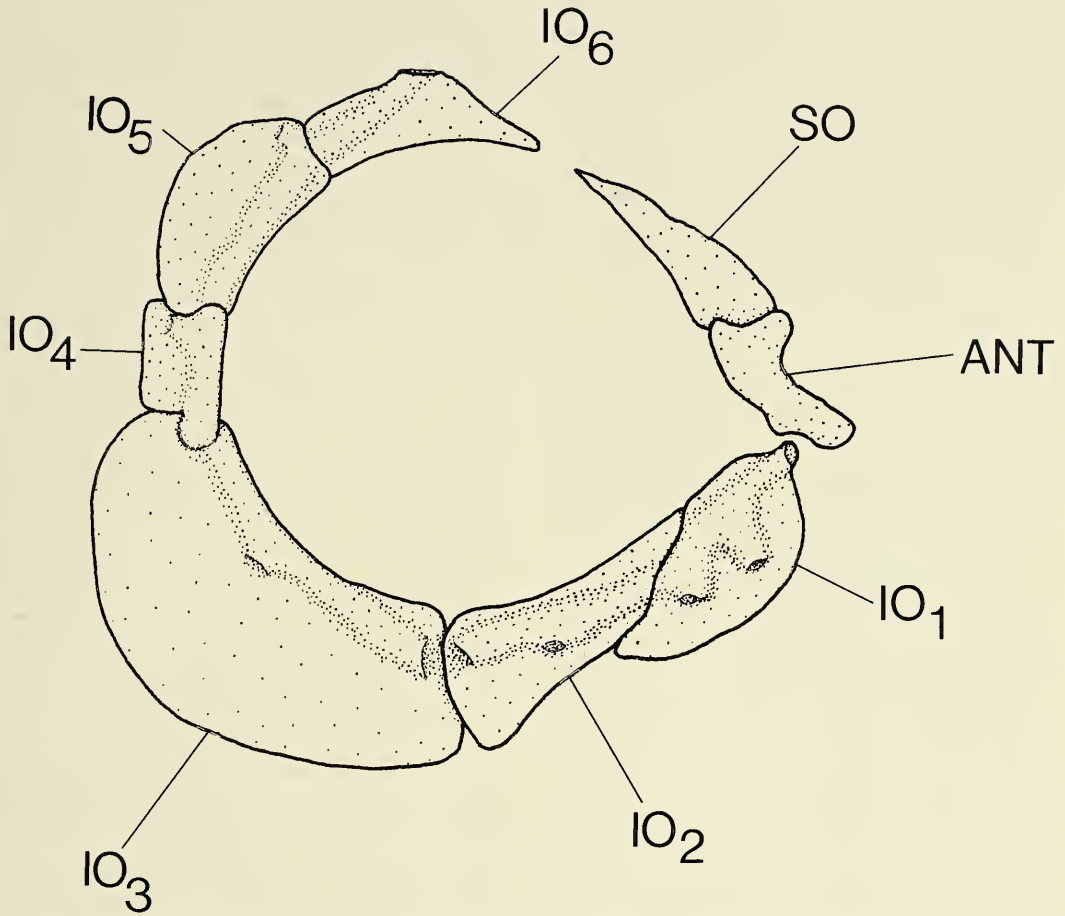


Fig. 2. Infraorbitals and supraorbital of *Moojenichthys myersi*, USNM 304497, 84.8 mm SL, right side, anterior to right. Abbreviations: ANT—antorbital; IO—infraorbitals (1 to 6); SO—supraorbital.

from other characids with expanded coracoids, we should note that the occurrence of such modifications of the infraorbitals extends beyond *Moojenichthys* and *Triporthus*. Howes (1982:5) illustrated a morphology of the first and second infraorbitals in *Brycon acuminatus* (Eigenmann & Norris) apparently comparable to that in *Moojenichthys* and *Triporthus*. At least some other species of *Brycon*, in contrast, have more generalized associations between the first two infraorbitals (e.g., *B. meeki*, see Weitzman 1962:fig. 8).

Brycon has been suggested to be a likely

close relative to *Triporthus* by both Regan (1911:18) and Weitzman (1960:243). In his overview of the former genus Howes (1982:1) questioned whether *Brycon* is monophyletic, but utilized the traditional concept of the genus until future phylogenetic and revisionary studies can be undertaken. In the absence of such phylogenetic data Howes excluded *Triporthus* from *Brycon* on the basis of the presence of the mid-ventral keel in the latter genus; noting that *Triporthus* shares, however, all the other diagnostic characters of *Brycon*. The various similarities between *Triporthus* and *Brycon* noted

by Regan, Weitzman, and Howes, and the derived features of the infraorbitals cited above for *Moojenichthys*, *Triportheus*, and at least some species of *Brycon*, raise the question of whether the lineage formed by *Triportheus* and *Moojenichthys* may be most closely related to some subunit of *Brycon*. Resolution of that question must await further revisionary and phylogenetic studies of both *Triportheus* and *Brycon*.

Autapomorphies of Moojenichthys myersi.—Within the lineage formed by *Moojenichthys*, *Triportheus*, and possibly *Brycon* or some subunit of the latter genus (see immediately preceding discussion), one of the more notable derived features for *Moojenichthys myersi* (hereafter referred to as *Moojenichthys*) is the absence of the single symphyseal tooth posterior to the main row of dentition on each dentary. Such symphyseal teeth are common to all members of *Triportheus* and *Brycon*, and also occur in *Chalceus* Cuvier. *Chalceus* shares all the defining characters of *Brycon*, but is excluded from *Brycon* because it possesses a supramaxilla (Howes 1982:1–2). An inner row of teeth on the dentary developed to varying degrees also occur in various characiforms in both the New World (e.g., Lebiasinidae, Weitzman 1964:143) and Africa (e.g., diverse genera in the Characidae, see Poll 1957:95, and Distichodontidae, Vari 1979:275–277). This broad phyletic distribution of symphyseal teeth both in groups proximate to *Moojenichthys* and other more distantly related characiforms, makes it most parsimonious to hypothesize that the absence of the symphyseal dentary teeth in *Moojenichthys* is a derived loss.

The ventrally recurved form of the maxillary dentition and the large number of teeth along the anterior margin of the maxilla distinguish *Moojenichthys* (Fig. 3) from all examined species of *Triportheus*. The ventrally recurved maxillary teeth in *Moojenichthys* are unique within the assemblage formed by that genus, *Triportheus*, and possibly *Brycon*, and are hypothesized to be an autapomorphy for *Moojenichthys*. In con-

trast, the large number of teeth (14 to 20) along the anterior margin of the maxilla in *Moojenichthys* is more difficult to evaluate. On the one hand that dentition does serve to readily separate *Moojenichthys* from *Triportheus* which has only 2 to 4 teeth in that series. Alternatively the species of *Brycon* have 10 to 30 teeth along the maxilla (Howes 1982:46), with most species overlapping the range in tooth number of *Moojenichthys* to some degree. This common occurrence of large numbers of maxillary teeth in *Moojenichthys* and *Brycon* raises the possibility that the relatively few maxillary teeth in *Triportheus* may be synapomorphic for the members of that genus, and that the high number of maxillary teeth in *Moojenichthys* is primitive.

A final noteworthy autapomorphy for *Moojenichthys* involves the anterior portion of the lateral ethmoids. In *Moojenichthys*, *Brycon* and *Triportheus* the anterior surface of the lateral ethmoid bears a distinct process that extends anteriorly and medially to contact the posterodorsal surface of the vomer (see Weitzman 1962:fig. 3 for an illustration of the condition in *Brycon meeki*). In *Moojenichthys* the anterior process of the lateral ethmoid is developed into an elongate anteriorly-tapering process (Fig. 4) that is significantly longer than comparable processes in *Triportheus* and *Brycon*. Anteriorly this elongate anterior process of the lateral ethmoid in *Moojenichthys* contacts a distinct lateral process situated on the dorsal surface of the vomer. The space between the anterior processes of the paired lateral ethmoids and dorsal of the vomer and parasphenoid is, in turn, filled by a large cartilage mass comparable to that in *Brycon*, *Triportheus*, and many other characids. Although the presence of the anterior process of the lateral ethmoid is not unique to *Moojenichthys*, the degree of the anterior elongation of the structure is not equalled in other examined characiforms and this modification is thus considered autapomorphic for the genus.

The relationship of the anterior process

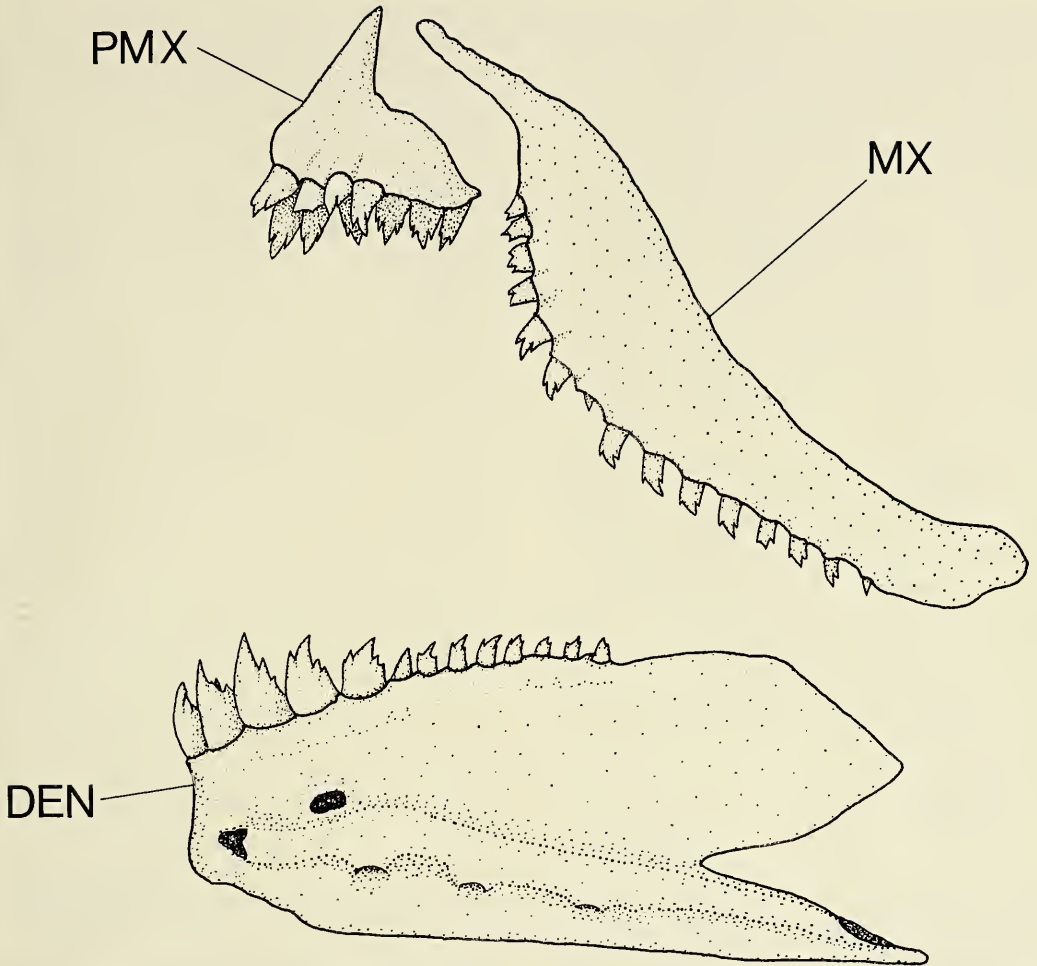


Fig. 3. Upper and lower jaws of *Moojenichthys myersi*, USNM 304497, 84.8 mm SL; left side, anterior to left; individual bones separated from positions in life. Abbreviations: DEN—dentary; MX—maxilla; PMX—premaxilla.

of the lateral ethmoid to the parasphenoid, vomer, and associated median cartilage in *Moojenichthys* is also distinctive. When present, the anterior process of the lateral ethmoid in characids usually extends directly along the lateral margin of the parasphenoid and vomer (e.g., *Brycon meeki*, see Weitzman 1962:fig. 3). *Moojenichthys*, in contrast, has a distinct vertical gap between the ventral margin of the anterior process of the lateral ethmoid and the dorsal surface of the vomer. This results in a broad lateral exposure of the median cartilage mass (Fig. 4). This relationship of the lateral eth-

moid and proximate bones and cartilages is unknown in *Triportheus*, *Brycon* and other examined characiforms, and is consequently hypothesized to represent an additional autapomorphy for *Moojenichthys*.

Moojenichthys Miranda-Ribeiro

Moojenichthys Miranda-Ribeiro 1956:546 [type *Moojenichthys myersi* Miranda-Ribeiro, by original designation].—Géry 1972:55 [possible derivation from *Brycon*].—Géry 1977:346 [similarities with *Triportheus* noted; dentition compared with that of “Tetraodoninae”].

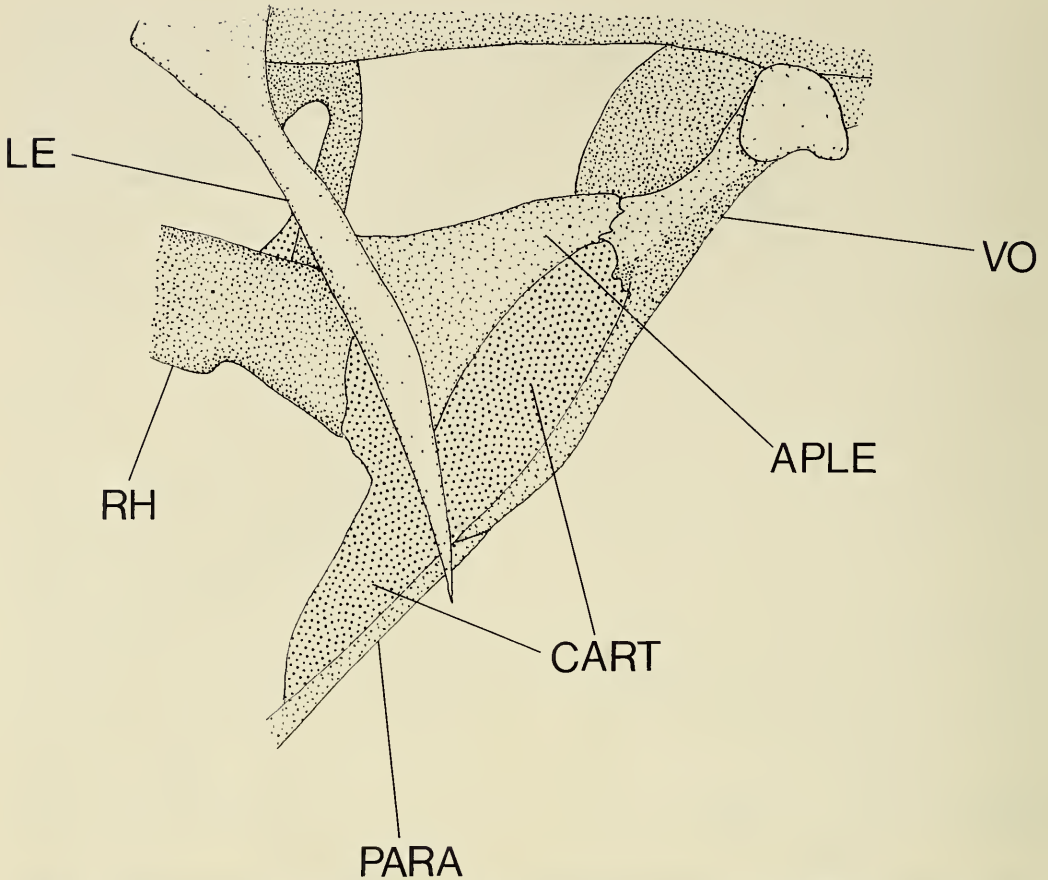


Fig. 4. Anterior portion of the neurocranium of *Moojenichthys myersi*, USNM 304497, 84.8 mm SL; right side, lateral view, anterior to right. Abbreviations: APLE—anterior process of lateral ethmoid; CART—cartilage; LE—main body of lateral ethmoid; PARA—parasphenoid; RH—rhinosphenoid; VO—vomer.

Diagnosis.—Within the clade formed by *Moojenichthys* and *Triporthesus* only the former genus lacks the paired symphyseal teeth posterior to the main row of dentary dentition. *Moojenichthys* also differs from *Triporthesus* in the numerous ventrally recurved teeth along the anterior margin of the maxilla, and in the derived degree of development and position of the anterior process of the lateral ethmoid. *Moojenichthys* can also be distinguished from *Triporthesus* on the basis of its possession of two rather than three rows of teeth on the premaxilla, and in having numerous teeth along much of the anterior margin of the maxilla rather than

several teeth limited to the dorsal portions of the maxilla.

Remarks.—The derived features described above are congruent with the hypothesis that *Moojenichthys* forms a monophyletic lineage with *Triporthesus*, or with *Triporthesus* and a subunit of *Brycon*. This conclusion raises the question of whether it is appropriate to continue to recognize a monotypic *Moojenichthys*, or whether that genus should be synonymized into *Triporthesus*.

Moojenichthys is characterized by a series of autapomorphic features. Within the Characiformes such phenetically distinct

taxa have been traditionally segregated into monotypic genera. We reject the criterion of phenetic distinctness as an a priori basis for the continued recognition of *Moojenichthys*, but nonetheless suggest that it is premature to synonymize *Moojenichthys* into *Triportheus*. Our decision is a consequence of the present poor knowledge of the phylogenetic relationships within *Triportheus*. Until such time as we have a rigorous hypothesis of the relationships within *Triportheus* it is impossible to hypothesize whether *Moojenichthys* is the sister-group to that genus, and thus could be preserved, or simply represents a subunit of *Triportheus*. In the latter case the continued recognition of *Moojenichthys* would result in a paraphyletic *Triportheus*. That problem could be resolved in one of several ways depending on the topology of the phylogenetic tree for the clade consisting of *Moojenichthys* plus *Triportheus*. *Moojenichthys* could be synonymized into *Triportheus* along with *Coscinoxylon*, a genus not presently recognized by most authors. Alternatively the topology of the phylogenetic tree might be such that it would be possible to continue to recognize *Moojenichthys* either by expanding the definition of the genus, or by recognizing one or more other genera in the clade in addition to *Triportheus* and perhaps *Coscinoxylon*. Given these diverse possibilities, we continue to use *Moojenichthys* in this study.

Moojenichthys myersi Miranda-Ribeiro
Figs. 1–7, Table 1

Moojenichthys myersi Miranda-Ribeiro, 1956:546–547, fig., type locality: “Braço River, Ilhéos [=Ilhéus], state of Bahia, Brazil.—Géry, 1977:346 [citation; possible relationships].

Diagnosis.—See “Diagnosis” of *Moojenichthys* above.

Description.—Morphometrics of holotype, paratype and larger examined non-type specimens presented in Table 1. Body elongate, distinctly compressed laterally in all

specimens greater than 25 mm SL, somewhat less so in smaller individuals. Greatest body depth located slightly anterior to vertical line through origin of pelvic fin, approximately equal to one-half length of longest pelvic-fin ray in specimens over 50 mm SL; body not as deep and mid-ventral keel less developed in smaller examined specimens. Dorsal profile of head slightly convex from margin of lip to vertical line through posterior nostril, nearly straight from that line to rear of head. Dorsal profile of body slightly convex from rear of head to origin of dorsal fin, posteroventrally slanted and somewhat convex along base of dorsal fin; straight from posterior termination of dorsal fin to adipose fin, and moderately concave along caudal peduncle. Dorsal portion of body obtusely keeled transversely anterior to dorsal fin; transversely rounded posterior to fin. Ventral profile of head distinctly convex over lip, straight along anteroventral margin of jaw, and distinctly convex ventral to joint with quadrate. Ventral profile of body irregular, distinctly convex overall; very slightly convex from isthmus nearly to vertical line through origin of pectoral fin; convexity greater from that line to origin of pelvic fin; straight to slightly concave from origin of pelvic fin to anterior termination of anal fin; straight and posterodorsally slanted along base of anal fin; slightly concave along dorsal peduncle. Distinct mid-ventral keel extending from isthmus to between origins of pelvic fins; keel less developed in specimens under 20 mm SL; increasingly obvious in individuals over 30 mm SL, most developed in specimens of over 50 mm SL. Scales along margin of keel flat, not folded over edge of keel.

Head obtusely pointed in profile; mouth terminal, lower jaw longer than upper, with dentigerous portion of maxilla distinctly angled posteroventrally. Maxilla extending posteriorly under orbit to vertical line through anterior margin of pupil. Nostrils of each side close together; anterior opening

Table 1.—Morphometrics of *Moojenichthys myersi*. Standard length is expressed in mm; measurements 1 to 14 are percentages of standard length; 15 to 18 are percentages of head length. Dashes indicate measurement that could not be taken due to damage to holotype. Range includes values for 24 specimens (holotype, MNRJ 4127; paratype MNRJ 4128; and 22 of the larger non-type specimens out of USNM 304497, MZUSP 40227, MNRJ 11605, and ANSP 164288), with the exception of length of the longest dorsal-fin ray which is based on 23 specimens, and length of the longest pectoral-fin ray which is based on 22 specimens.

	Holotype	Paratype	Range	Mean
Standard length	96.6	85.8	27.0–96.6	69.1
1. Greatest body depth	25.7	25.5	22.2–28.7	27.0
2. Snout to dorsal-fin origin	65.2	62.0	60.7–65.4	62.8
3. Length of base of dorsal fin	8.2	7.5	7.1–8.7	7.8
4. Posterior terminus of dorsal fin to adipose fin	18.0	17.8	16.4–19.8	18.0
5. Posterior terminus of dorsal fin to caudal-fin base	28.9	29.6	27.9–32.4	29.8
6. Snout to origin of pelvic fin	49.6	50.5	46.7–51.3	49.2
7. Snout to origin of anal fin	68.7	67.6	62.2–68.7	65.3
8. Length of base of anal fin	31.5	28.3	28.1–32.1	30.4
9. Length of caudal peduncle	8.7	9.8	8.0–10.6	9.2
10. Length of longest dorsal-fin ray	16.8	15.3	15.3–18.6	16.8
11. Length of longest pectoral-fin ray	—	32.1	24.4–32.1	30.1
12. Length of longest pelvic-fin ray	14.7	13.6	11.1–15.0	13.5
13. Least depth of caudal peduncle	7.6	7.0	6.3–8.7	7.9
14. Head length	24.1	24.2	23.7–29.0	24.6
15. Snout length	23.6	22.6	20.0–27.0	23.5
16. Orbital diameter	36.1	36.5	31.7–38.9	36.3
17. Postorbital head length	38.2	36.5	29.3–41.8	38.1
18. Interorbital width	24.0	24.0	19.1–27.6	24.5

circular, posterior kidney-shaped. Eye relatively large, without adipose eyelid. Median fronto-parietal fontanel well developed; completely separating parietals; frontals in contact only anteromedially and at epiphyseal bar. Fontanel becoming progressively wider posteriorly, extending onto dorsomedial surface of supraoccipital.

Infraorbital series complete (Fig. 2), all infraorbitals with laterosensory canal segments. Sixth infraorbital (dermosphenotic) with single tubular laterosensory canal segment. First infraorbital expanded anteroventrally, with distinctly convex anterior margin, anterior portion extends over lateral surface of maxilla; laterosensory canal segment with three sections in larger specimens. Supraorbital and antorbital present.

Four branchiostegal rays, first three attached to anterior ceratohyal, fourth to posterior ceratohyal. Gill-rakers relatively elongate, 17 or 18+1+40 to 42 rakers on

outermost gill-arch (in 2 larger cleared and counterstained specimens).

Lower jaw with one row of 12 to 14 teeth on each side on each dentary (Fig. 3); number of teeth greater in largest specimens; inner row consisting of single symphyseal tooth absent. Anterior 5 teeth on dentary notably larger than remainder, with 5 cusps, medial cusp distinctly largest. Remaining teeth usually tricuspidate, rarely unicuspidate, with largest cusp recurved somewhat posteriorly. Teeth on premaxilla in two rows; teeth of inner row larger (Fig. 3). Four tricuspidate teeth of approximately equal size in outer row. Six teeth in inner row on premaxilla; 2 medial teeth largest, subequal; remaining teeth gradually becoming smaller laterally; medial tooth tricuspidate, remaining teeth in row with 5 cusps. Lateral tooth of inner row of premaxilla approximates dorsal tooth on maxilla. Anterior margin of maxilla distinctly convex, with single row

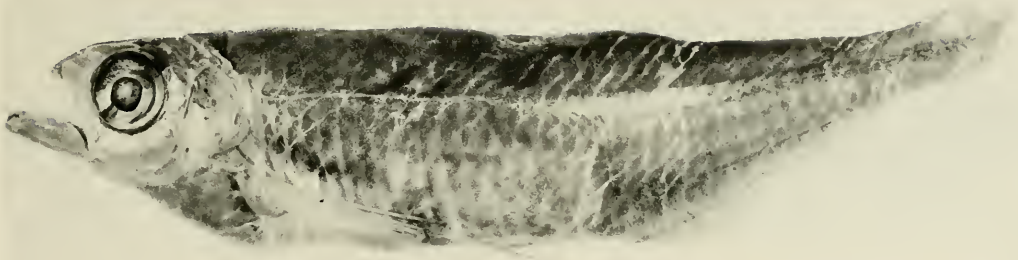


Fig. 5. *Moojenichthys myersi*, Brazil, Bahia, "Braço river" [=Rio do Braço], Ilhéos [=Ilhéus]; MNRJ 4127, holotype, 96.6 mm SL.

of teeth (Fig. 3). Teeth on maxilla distinctly smaller than smallest tooth on premaxilla; typically unicuspidate in specimens of approximately 27 mm SL, bicuspidate or usually tricuspidate in specimens of about 40 mm SL and greater. Smaller specimens with 2 to 9 teeth limited to upper one-quarter to one-half of anterior margin of maxilla; larger specimens with 14 to 20 teeth arranged along nearly entire anterior margin of maxilla. Largest cusp of teeth on maxilla recurved ventrally.

Scales cycloid, thin, relatively large. Lateral line distinctly decurved ventrally, completely pored from supracleithrum to base of middle rays of caudal fin. Forty to 43 [42] scales in lateral line (70% of specimens with 42 scales); 6 or 7 [7] scales in transverse series from origin of dorsal fin to lateral line; 3 or 4 [3] scales in transverse series from origin of pelvic fin to lateral line (4 scales present in only 1 specimen); 3 or 4 [3] scales in transverse series from origin of anal fin to lateral line; 17 to 21 [20] scales along mid-dorsal line between tip of supraoccipital process and origin of dorsal fin (60% of specimens with 19 or 20 scales); 9 or 11 [11] scales along mid-dorsal line between posterior termination of dorsal fin and adipose fin (91% of specimens with 10 or 11 scales); 13 to 15 [13] horizontal scale rows around caudal peduncle (86% of specimens with 14 or 15 scales).

Dorsal-fin rays ii,8 or 9 or iii,9 [ii,9] (ii,9

most common); anal-fin rays iv,31 to 35, or v,33 [iv,33] (iv,33 most common); pectoral-fin rays i,9 to 12 followed by 0 to ii unbranched rays [i,10,i] (i,10,i most common); pelvic-fin rays i,6 [i,6]; principal caudal-fin rays 10/9 [10/9].

Dorsal fin profile obtusely acute, posterior unbranched and first branched ray subequal; posterior unbranched ray typically slightly longer. Dorsal fin situated on posterior half of body; origin of fin located slightly posterior of vertical line through anterior terminus of anal fin, closer to base of caudal fin than to tip of snout. Longest dimension of adipose fin approximately equal to horizontal width of pupil; origin of adipose fin slightly anterior of vertical line through posterior terminus of anal fin. Pectoral fin large, profile distinctly acute; when fin depressed, tip extends to vertical line approximately two-thirds distance along pelvic fin. Pelvic fin profile obtusely acute, origin of fin at posterior margin of mid-ventral keel, tip of depressed fin extending posteriorly slightly beyond anus, but falling short of anterior terminus of anal fin. Axillary pelvic scale present, its length about one-third that of longest pelvic-fin ray. Cleared and counterstained 84.8 mm SL male with 6 to 15 basally directed bony hooks along posterior margins of first 5 branched pelvic-fin rays. Ventral margin of anal fin somewhat rounded anteriorly, with last unbranched and first branched rays

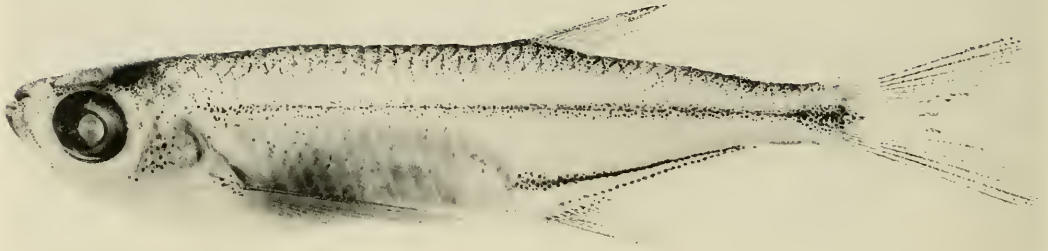


Fig. 6. *Moojenichthys myersi*, Brazil, Bahia, Rio do Braço, 2 km SW of town of Rio do Braço, on Fazenda Luzia, USNM 304496, 33.4 mm SL.

longest, subequal, following 10 to 12 branched rays rapidly decreasing in length, remaining anal-fin rays slowly decreasing in length. Males with 1 to 8 basally-directed bony hooks along posterior margins of distal sections of 7 to 14 longest anal-fin rays. Caudal fin forked, lobes obtusely pointed.

Total vertebrae 39 (2), 40 (20), 41 (2) [40].

Color in life.—Descriptions based on color transparencies of a series of recently preserved specimens captured in August 1988 and February 1989. Overall coloration of specimens ranging from 15.9 to 33.4 mm SL clear to yellowish. Iris, lower jaw, infraorbital region, opercle, and peritoneum silvery. Tip of lower jaw, snout, dorsal portions of body and basal portions of caudal fin light yellow. Traces of yellow pigmentation apparent on dorsal, adipose, and anal fins. Other fins hyaline. Mid-lateral dark stripe on body quite obvious, but somewhat masked anteriorly by guanine. Dark stripe above anal fin, and dark pigmentation on all fins clearly visible.

Specimens above approximately 50 mm SL bright silver overall, somewhat darker along dorsal portions of head and body. Dense guanine on scales completely masking both dark stripes along mid-lateral surface of body, and those on ventrolateral surface of body above anal fin. Dark pigmentation on fins as in preserved specimens.

Coloration in preservative.—Overall

ground color of specimens fixed in formalin and lacking guanine on scales yellowish brown. Dense fields of small, dark chromatophores on upper lip, snout, and dorsal surface of head (Figs. 5–7). Very intense, horizontally elongate stripe of dark pigmentation along dorsal portion of lower lip; less intense dark pigmentation ventral to this on lower jaw. Scattered small dark chromatophores on lateral surface of head anterior to orbit and on opercle; pigmentation more obvious in specimens totally lacking guanine on head.

Body with mid-lateral stripe of small, dark chromatophores extending from supraclithrum posteriorly to caudal peduncle; stripe gradually expanding vertically posteriorly; broadened into distinctly wider diffuse dark spot on lateral surface of caudal peduncle. Body dorsal of dark mid-lateral stripe with margins of scales outlined by dark chromatophores; pattern most obvious in medium sized specimens, somewhat obscured by overall dusky appearance of dorsal portions of body in larger specimens. Stripe of dark chromatophores extending posterodorsally along ventrolateral portion of body from slightly anterior of vertical through anterior terminus of fin posteriorly to posterior terminus of fin. Stripe wider and distinctly separated from base of anal fin anteriorly, becoming gradually narrower and approaching base of anal-fin rays posteriorly.



Fig. 7. *Moojenichthys myersi*, Brazil, Bahia, Rio do Braço, 2 km SW of town of Rio do Braço, on Fazenda Luzia, MZUSP 40227, 81.6 mm SL.

Dorsal fin with dense field of dark chromatophores along distal portions of rays and membranes. Margins of adipose fin in larger specimens outlined by scattered dark chromatophores. Anterior rays of pectoral and pelvic fins outlined by series of small dark chromatophores. Anterior margin and distal portions of anal fin dusky, most rays outlined distally by dark chromatophores. Caudal fin dusky in specimens of all sizes, rays outlined by series of small dark chromatophores.

Common names.—Brazil, Bahia, Ilhéus: “Mossarupê,” “Piaba-faca,” and “Canivete” (Miranda-Ribeiro, 1956:547). During the 1988 and 1989 expeditions the only name used by local fishermen was “Piaba-faca.”

Ecology.—Specimens collected during the 1988 and 1989 expeditions were collected in black waters containing limited suspended material. The area surrounding the river was originally a portion of the Atlantic Coastal Forest, but much of the understory vegetation has been replaced by cocoa trees. In the areas sampled for fishes the Rio do Braço was between 10 and 25 m wide, ranged from 1.5 to 3 m deep, and had mats of floating vegetation along its margins. The bottom was sandy-mud with scattered boulders.

Other fishes captured with *Moojenichthys*

myersi and the families to which they are presently assigned were *Steindachnerina elegans* (Curimatidae); *Nematocharax venustus*, *Oligosarcus macrolepis*, *Astyanax* sp., *Characidium* sp. (Characidae); *Hoplias* sp. (Erythrinidae); *Rhamdia* sp. (Pimelodidae); *Poecilia* sp. (Poeciliidae); *Astronotus ocellatus* and *Geophagus brasiliensis* (Cichlidae). The *Astronotus ocellatus* record represents an introduction.

Diet.—Examination of the stomach contents of the three cleared and counterstained specimens shows that the species eats mosquito larvae and other aquatic invertebrates.

Distribution.—Known only from the Rio do Braço in the state of Bahia, Brazil. The original description of *Moojenichthys myersi* states that the type material was collected in the “Braço river, Ilhéus.” In actuality the mouth of the “Braço river” [=Rio do Braço] is located approximately 7 km along the coast north of the city of Ilhéus (“Ilhéos” of Miranda-Ribeiro). Limited ichthyological collecting has taken place in the Bahian coastal drainages near the Rio do Braço. Thus the lack of records of *Moojenichthys myersi* from other neighboring river systems may be a consequence of poor sampling.

Material examined.—Brazil. Bahia: “Braço river,” Ilhéus [=Ilhéus], MNRJ

4127, 1 specimen, holotype, 96.6 mm SL; same locality, MNRJ 4128, 1 specimen, paratype, 85.8 mm SL; Ilhéus, Fazenda Pirataquicê, MNRJ 5572, 1 specimen, 78.2 mm SL (locality not found in examined gazetteers or maps); Rio do Braço, 2 km SW of town of Rio do Braço (approx. 14°39'S, 39°16'W), on Fazenda Luzia, USNM 304497, 9 specimens, 20.5–84.8 mm SL (1 specimen, 84.8 mm SL, cleared and counterstained); USNM 304496, 15 specimens, 17.8–33.4 mm SL (1 specimen, 27.0 mm SL, cleared and counterstained); MZUSP 40226, 15 specimens, 15.9–30.5 mm SL; MZUSP 40227, 9 specimens, 19.6–84.1 mm SL (1 specimen, 56.0 mm SL, cleared and counterstained); ANSP 164287, 3 specimens, 17.4–26.5 mm SL; ANSP 164288, 2 specimens, 63.4–76.0 mm SL; MNRJ 11604, 3 specimens, 20.1–24.4 mm SL; MNRJ 11605, 2 specimens, 63.4–74.9 mm SL.

Comparative cleared and stained material examined. — *Brycon falcatus*, USNM 226161, 2 specimens. *Carnegiella strigata*, USNM 225245, 5 specimens. *Clupeacharax anchoveoides*, USNM 302245, 1 specimen. *Cynodon gibbus*, USNM 270338, 2 specimens. *Engraulisoma taeniatum*, USNM 302225, 1 specimen. *Gasteropelecus sternicla*, USNM 226337. *Gnathocharax steindachneri*, USNM 278995, 2 specimens. *Rhaphiodon vulpinus*, USNM 231549, 3 specimens. *Triportheus angulatus*, USNM 270343, 2 specimens. *Triportheus* sp., USNM 280498, 4 specimens; USNM 258079, 2 specimens.

Acknowledgments

A number of the specimens of *Moojenichthys myersi* that served as the basis for this paper was collected during a collaborative FFCLRP-USP and USNM expedition in the state of Bahia, Brazil. The success of the collecting effort was assured by the enthusiasm of Susan L. Jewett (USNM), Hertz F. Santos, Maura H. Manfrin, Eliseu B. Dias,

and Eduardo Castadelli, Jr. (all of FFCLRP-USP) who unstintingly assisted in the often difficult fishing efforts. Hertz F. Santos made a special second trip into the region of the type-locality to collect additional material of the species, including an extensive series that included most of the larger individuals reported on in this paper. Figures 5 to 7 were prepared by Mr. Theophilus B. Griswold. Sandra Raredon and Jeffrey Howe assisted in the research efforts at USNM. Ms. India Moreira (MNRJ) arranged for the loan of the holotype and paratype of *Moojenichthys myersi*, and Mr. Luis Paulo S. Portugal (MZUSP) and Dr. Naércio A. Menezes (MZUSP) facilitated our examination of those specimens. This paper was improved by the suggestions of Dr. Stanley H. Weitzman (USNM), Dr. Wayne C. Starnes (USNM), Dr. William L. Fink (University of Michigan, Museum of Zoology), Dr. Darrell J. Siebert (British Museum (Natural History)), and Mrs. Marilyn Weitzman (USNM). We thank all of the above for their assistance.

Extensive logistical support for the expedition that collected most of the specimens of *Moojenichthys myersi* was provided by FFCLRP-USP. Funding for that collecting effort was provided through the Neotropical Lowland Research Program of the International Environmental Sciences Program of the Smithsonian Institution. That program also supported the research associated with this project both at museums in Brazil and at the Smithsonian Institution.

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